EQUILIBRIUM OR NON-EQUILIBRIUM ECOSYSTEMS? SCALING EFFECTS IN RANGELAND ECOSYSTEMS OF WESTERN MONGOLIA

With 5 figures

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Aride Weideökosysteme, räumlicher Maßstab, Landschaft, Pflanzengesellschaft, Population, Bodennährstoffe

Zusammenfassung: Equilibrium- oder Non-Equilibrium-Ökosysteme. Maßstabseffekte in Weideökosystemen der Westmongolei In der Diskussion von Equilibrium- vs. Non-Equilibrium-Dynamik von Weideökosystemen hat die Berücksichtigung verschiedener Maßstabsebenen jüngst zur Forderung nach Integration beider Konzepte geführt. Vorliegende Studie untersucht den Beweidungseinfluss in den ariden Wüstensteppen der Westmongolei auf drei räumlichen Maßstabsebenen. Auf der Landschaftsebene wird der Beweidungseinfluss auf die die Vegetation bestimmenden Faktoren beurteilt und beweidungsbedingte Pflanzengesellschaften gesucht. Auf der Ebene von Pflanzengesellschaften werden Gesamtartenzahl, Deckung der Gesamtvegetation, Anteil und Deckung annueller Arten sowie Bodennährstoffparameter entlang von Gradienten abnehmender Weideintensität untersucht. Auf der Populationsebene werden Bestandsdichte, Gesamtbiomasse und der Anteil blühender Exemplare des Zwergstrauches Artemisia xerophytica ebenfalls entlang von Weidegradienten geprüft. Die Ergebnisse zeigen einen zunehmenden Beweidungseinfluss mit abnehmendem räumlichen Maßstab. Während auf der Landschaftsebene kein Weideinfluss nachgewiesen werden konnte, reagieren die Vegetationsparameter unterschiedlich auf Beweidung und unterschiedlich in den einzelnen Pflanzengesellschaften. Auf der Populationsebene reflektieren die Ergebnisse deutlich den Weidegradienten in Übereinstimmung mit dem Equilibrium-Modell. Die Studie zeigt equilibriale und non-equilibriale Eigenschaften von ariden Wüstensteppen in Abhängigkeit vom Untersuchungsmaßstab. Die Notwendigkeit mehrerer Maßstabsebenen zur Bewertung von Vegetationsdynamik und Beweidungseinfluss wird dargestellt. Darüber hinaus wird vorgeschlagen, zukünftige Forschungen in einem Vergleich von Landschaften mit und ohne Co-Evolution von Herbivorie durchzuführen.

Summary: For many years, rangeland ecologists have debated about whether the state of semiarid and arid pastures is the expression of an ecological equilibrium dynamics reached in response to grazing livestock. Since the problem having been considered at different spatial scales, it is recognised that the competing concepts of equilibrium and non-equilibrium dynamics need to be integrated. The present study assesses grazing influence in Mongolia's arid desert steppe at three spatial scale levels. At the landscape level, the investigation focused on the impact of grazing on vegetation-determining ecological factors and on the occurrence of grazing-mediated plant communities. At the community level, the total number of species, the total vegetation cover, the percentage of annual species, the cover of annual species, and the soil nutrient properties were assessed along gradients of grazing intensity. At the population level, the total number and weight of plants per plot, individual plant weight and the proportion of flowering plants of the dwarf semishrub Artemisia xerophytica were recorded along gradients of grazing intensity. The results show that grazing influence increases with decreasing spatial scale. At the landscape level, no grazing influence could be identified. At the community level, different vegetation parameters respond to grazing in different ways, and the responses of the same parameters vary between plant communities. At the population level, the results clearly reflect the grazing gradient in the way predicted by the equilibrium model. The study demonstrates that even arid desert steppes display equilibrial and non-equilibrial properties, depending on the observational scale. As a consequence, the assessment of vegetation dynamics and grazing impact in rangelands requires a multiple-scale approach that duly considers climatic differences. It is further suggested, that future research should draw comparisons between landscapes that co-evolved with herbivory, and those that did without.

1 Introduction

Since the mid-1980s, when sufficient data on the interference of grazing, climatic variability and vegetation dynamics of Africa's arid regions became available, researchers have challenged the previously common view that pastoral ecosystems used as commons are generally overstocked and mismanaged (HOME- WOOD a. RODGERS 1987; ELLIS a. SWIFT 1988; BEHNKE a. SCOONES 1993). Rangeland dynamics has since been the object of much controversy. Prominent topics of the debate are the influences of rainfall variability, herbivory and vegetation dynamics in arid and semiarid pastoral systems, especially in Africa and Australia (VETTER 2005). The main dispute runs between two models of ecosystem dynamics. The equilibrium model (EM), referring to grazing-sensitive systems with low rainfall variability, regards livestock density as the primary driver of vegetation dynamics (ILLIUS a. O'CONNOR 1999). The non-equilibrium model (NEM), referring to grazing-resilient systems with high climatic variability, suggests that, since food supply can never be exceeded by grazing demand, vegetation dynamics is decoupled from livestock density and primarily determined by stochastic abiotic factors (ELLIS a. SWIFT 1988; BEHNKE a. SCOONES 1993; SULLIVAN a. ROHDE 2002). The EM, which is based on CLEMENTS' (1916) concept of plant succession, allows applying carrying capacity concepts, including optimal management strategies, to pastoral systems where rainfall and hence forage production are predictable. The NEM, on the other hand, is based on a irreversible state-and-transition dynamics of vegetation (WESTOBY 1980; ALLEN-DIAZ a. BARTOLOME 1998). It rejects the concept of carrying capacity and supports mobile stocking regimes for systems with high climatic variation and hence unpredictable primary production (WESTOBY et al. 1989; ELLIS a. SWIFT 1988; BEHNKE a. SCOONES 1993). In the controversy over the two models, little attention has been paid to the differences in climate, the associated differences in vegetation structure, and the land use regimes of the investigated regions. Furthermore, the two models were considered as mutually exclusive (SULLIVAN a. ROHDE 2002).

Recent studies have shown that one ecosystem can display EM as well as NEM characteristics, depending on the scale of observation (OBA et al. 2003). Therefore, a scale-sensitive synthesis of the two models has been called for (BRISKE et al. 2003; OBA et al. 2003; VETTER 2005).

In Mongolia, the privatisation of state-owned cooperatives has led to a considerable increase of mobile livestock-keeping (MEARNS 1993; JANZEN a. BAZARGUR 2003). Economic and social infrastructure in rural areas collapsed, leading to a concentration of herders near administrative centres (BATKHISHIG a. LEHMKUHL 2003; JANZEN 2005). Seen against the backdrop of the associated risks of overgrazing and degradation, it is pivotal for sustainable resource use and conservation policy in Mongolia to understand the impacts of grazing on the country's arid ecosystems, and to identify the relevance of both concepts.

Their applicability to Mongolia has been tested in a small number of studies (FERNANDEZ-GIMENEZ a. ALLEN-DIAZ 1999, 2001; STUMPP et al. 2005; WESCHE a. RETZER 2005). The results indicate that neither of the models describes the dynamics of desert steppes and dry steppes sufficiently; but the empirical data better conform to the NEM. No previous study on grazing impacts in Mongolia considered the effect of spatial scale in its investigation approach.

The present study examines the grazing impact in desert steppes of western Mongolia at three spatial



Fig. 1: Location of the study area in Western Mongolia (Sources: Tibet Family Tours and Travel; KRETSCHMER 2004, modified)

Lage des Untersuchungsgebietes in der Westmongolei (Quellen: Tibet Family Tours and Travel; KRETSCHMER 2004, verändert)

scale levels. At the landscape level, it assesses the impact of grazing on ecological factors, which were identified as the primary drivers of vegetation development by ZEMMRICH (2006) and tries to identify grazing-mediated plant communities. At the community level, it examines the impact of grazing on vegetation structure and soil nutrients within three different communities. At the population level, it assesses the influence of grazing on selected characteristics of the dwarf semishrub *Artemisia xerophytica*.

2 Material and sampling methods

2.1 Study area

The study area extends 55 km eastward from the shores of Lake Khar Us Nuur in the Great Lake Basin to the Argalant Mountains, near the northeastern border of Khovd province (Fig. 1). Located on the leeward side of the Altai Mountains, the area receives 62 mm mean annual precipitation with high interannual variations. The extreme continental climate is characterised by long, cold, dry winters and short, hot summers. 70–90% of the annual precipitation falls in summer (Climate station Dörgön, see Fig. 1).

The prevailing soil type is a gravel-rich, shallow Haplic Calcisol.

The sparse vegetation of the desert steppe (cf. ZEMMRICH 2005) is dominated by semishrubs, perennial bunchgrasses, and alliaceous geophytes of the genus *Allium*. In rainy summers, annual grasses and herbs prevail temporarily. The vegetation of the study area is a species-poor desert steppe with 9–12 species per 100 m² representing the typical plant communities of western Mongolia (HILBIG 1995; KHMELEV 2002).

Herders traditionally use the lower parts of the study area as spring pastures and the higher-lying parts as winter pastures. After privatisation, between 1990 and 1999, livestock numbers in the district increased by 36%. In three consecutive years between 1999 and 2002, heavy snowfalls followed by droughts and a significant migration of herders to urban centres, especially Ulaanbaatar reduced numbers to a level below that of 1985 (Statistics Agency of Khovd Province).

2.2 Sampling methods and data analysis

Data sampling and analyses were carried out at landscape, community and population scale, because they represent the wide span of spatial scale levels that expresses the vegetation properties relevant for grazing. Data on vegetation and soil were collected along several gradients of grazing intensity in an otherwise homogenous area. Each transect started at a livestock camp ground and lead up to 2.5 km away. A livestock camp ground is that part of a yurt camp (yurt: traditional nomad tent) in which sheep and goats, the most common livestock in the study area, are rounded up every night to protect them against wolves and the cold. Grazing intensity is highest near the camp grounds and decreases with the distance (KENTER 2005) and thus sampling areas in different grazing states are provided.

For an ecologically oriented classification, vegetation relevés were conducted following ELLENBERG (1956) and included potentially vegetation-determining environmental variables such as altitude, slope aspect and inclination, meso- and microrelief, water regime, influences of natural and anthropogenic disturbances, type of land use and distance to grazing hot spot. Soil samples were collected from homogenous sites comprising about five relevés each, and tested for pH, CaCO₃, N, C_{org}, electric conductivity (EC), CEC_{eff}, P and soil texture as reported by ZEMMRICH et al. (2007). To allow comparability and a general description of the little known soils of western Mongolia, soil analyses except for P concentration follows German standards (DIN 2000). To detect plant-available phosphorus, P was analysed according to HEINRICH (1987). The distance between sampling plots and livestock camp grounds was measured using GIS.

The derivation of vegetation driving environmental factors follows the concept of plant communities according to KOSKA et al. (2001), which integrates a floristic classification of vegetation with a classification of corresponding environmental conditions and thus enables the detection of vegetation driving variables. It was carried out in a combination of clustering for plant species sorting and tabular treatment according to (ELLENBERG 1956) supported by descriptive statistics and an analysis of variance (ANOVA) for floristic and corresponding environmental data. To validate classification results, floristic data were subjected to a Detrended Correspondence Analysis (DCA) and environmental data to a Principal Component Analysis (PCA) as ordination techniques suggested by (ØKLAND 1996; VAN DER MAAREL 2005).

In 20 additional 100 m^2 plots, located within the area covered by the *Artemisia xerophytica* plant community, the total number of *A. xerophytica* specimens was recorded along the grazing gradient described above. Additionally, the total above-ground biomass of all *A. xerophytica*, the proportion of their flowering plants and the average weight of the individual plants were determined (in 18 of the 20 plots). To distinguish between grazing effects and edaphic influences, soil samples from eight of the 20 *Artemisia xerophytica* plots were tested for parameters described above.

In the present study, a total of 169 vegetation relevés and 35 soil samples were evaluated.

Further methods used in the statistical analysis are described in Chapter 3.

3 Results

3.1 Landscape level

The main ecological factors determining vegetation composition and cover in the study area are identified by ZEMMRICH (2006). They comprise the general moisture supply and climate represented by altitude, the availability of edaphic moisture and water represented by soil texture, gravel concentration, soil salinity, topographic position, and competitive conditions represented by adaptation of species inventory to disturbances by water and by sediment erosion (Fig. 2). Grazing-mediated plant communities could be identified neither in close proximity to livestock camp grounds where they most of all expected nor in a wider distance. This is probably due to the fact that these vegetation-determining factors are insensitive to grazing.

3.2 Community level

Four plant communities were identified by ZEMMRICH (2006); three of them are examined in this paper (Fig. 2). They represent environmentally homogenous sites. Therefore, changes in vegetation properties can be interpreted as the result of different grazing intensities.

Because vegetation and soil data are not normally distributed, their correlation with the distance from the livestock camp ground was calculated by means of the Spearman rank correlation (R_s).



Fig. 2: Factor diagram of desert steppe (italic: recorded environmental parameters, bold capital: derived vegetation-determining ecological factors, bold underlined: classified plant communities, standard: site description of classified plant communities)

Faktorendiagramm der Wüstensteppe (kursiv: aufgenommene Umweltparameter, fett in Großbuchstaben: abgeleitete vegetationsbestimmende ökologische Faktoren, fett unterstrichen: klassifizierte Pflanzengesellschaften, Standard: Standortsbeschreibung der Pflanzengesellschaften)

In all plant communities, only the total vegetation cover and the percentage of annual species were significantly but weakly correlated with grazing intensity. While in the *Anabasis brevifolia-Allium mongolicum* desert steppe, the correlations of all vegetation parameters with grazing intensity are negative, they change from positive to negative in the *Artemisia xerophytica* semishrub desert steppe and from negative to positive in the *Krascheninnikovia ceratoides* shrub desert steppe (Fig. 3).

In all communities, the values of the vegetation parameters show considerable variation at similar distances from the livestock camp grounds.

Among the soil parameters, only C_{org} and N concentrations in the *Anabasis brevifolia-Allium mongolicum* desert steppe and the *Krascheninnikovia ceratoides* shrub desert steppe show a significant, strong negative correlation with grazing intensity, whereas P concentrations are not correlated in any community. Both C_{org} and N concentrations show a clear trend over the first 400 m of

the transect in the Anabasis brevifolia – Allium mongolicum desert steppe. In the Krascheninnikovia ceratoides shrub desert steppe, a continuous downward trend extends over the entire transect. However, the absolute concentrations of C_{org} and N are very low (Fig. 4).

3.3 Population level

The investigation at population scale was carried out in the *Artemisia xerophytica* semishrub desert steppe, the community least affected by grazing at community scale (cf. Fig. 3, Fig. 4). Vegetation data and soil nutrient values were tested for correlation with the grazing gradient by means of Spearman rank correlation (R_s), because data was not normally distributed and a linear correlation could not be assumed. Furthermore, soil data were used to differentiate edaphic from grazing influences.



Fig 3: Selected parameters of vegetation structure along the grazing gradient in plant communities of desert steppe Ausgewählte Parameter der Vegetationsstruktur entlang des Weidegradienten in den Pflanzengesellschaften der Wüstensteppe



Fig. 4: Selected soil parameters along the grazing gradient in plant communities of desert steppe Ausgewählte Bodenparameter entlang des Weidegradienten in den Pflanzengesellschaften der Wüstensteppe

While the soil nutrient concentrations remain constantly variable without a clear trend (Fig. 4), the values of all vegetation parameters increase over the first 800 m and display a clearly significant correlation with grazing intensity (Fig. 5). The total number of specimens, the total weight of the above-ground biomass, and the percentage of flowering specimens in *A. xerophytica* decrease near plot 12 at a distance of 900–1,000 m from the livestock camp ground. This effect can be attributed to the high local soil salinity (EC 9 mS/cm). From 1,000 m onwards, the general upward trend in the vegetation parameters is not uniform and may represent natural variation caused by intraspecific competition due to increased stand density (cf. ZEMM-RICH et al. 2007).

4 Discussion and conclusions

The identification of vegetation-determining factors and the assessment of their effects for each environmentally homogenous plant community individually make it possible to separate grazing from edaphic influences at all spatial scale levels, as postulated by FERNANDEZ-GIMENEZ and ALLEN-DIAZ (2001).

The grazing impact becomes more apparent as the spatial scale decreases¹), which matches the findings of OBA et al. (2003). While no grazing effect could be identified on the landscape level, the results on the community level contain partly statistically significant correlations of grazing intensity with vegetation parameters and clearly significant correlations with soil parameters. Different vegetation parameters respond to grazing in different ways (FERNANDEZ-GIMENEZ a. ALLEN-DIAZ 1999). Furthermore, a vegetation parameter may have different patterns in different communities. Significant correlations of grazing intensity with soil nutrient concentrations indicate eutrophication in two communities and thus points at an indirect influence of grazing on vegetation. The study reaffirms the findings of STUMPP et al. (2005) in Mongolia's dry

¹⁾ In this paper, in contrast to the usage of the terms in cartography, 'large scale' means a large area (= small map scale), and 'small scale' means a small area (= large map scale).



Fig. 5: Salinity and selected structural parameters of Artemisia xerophytica semishrubs along the grazing gradient (filled circles: structural parameters, open circle: salinity, number atop circle: plot number)

Salinität und ausgewählte Strukturparameter von Artemisia xerophytica-Sträuchern entlang des Weidegradienten (gefüllte Kreise: Strukturparameter, offene Kreise: Salinität, Nummer auf Kreis: Plot-Nr.)

steppe, who detected no changes in vegetation parameters near a grazing hot spot, but a significant increase in the concentration of soil nutrients like C_{tot} . N and P. This is contradicted by our findings at the population level. The edaphic conditions in the *Artemisia xerophytica* community were homogenous, except for the salinity peak at plot 12. However, at least to a distance of 800 m all recorded parameters of the *Artemisia xerophytica* population indicate the grazing gradient (Fig. 5) consisting of a direct impact through defoliation and trampling.

The results at landscape level match most community-level findings from other studies on in Mongolia's desert steppe and dry steppe that failed to detect a change in prevailing vegetation parameters (biomass, functional group cover, species richness, diversity along a grazing gradient: FERNANDEZ-GIMENEZ a. ALLEN-DIAZ 1999; species composition, species richness, above-ground standing biomass production in grazed and ungrazed plots in different years: WESCHE a. RET-ZER 2005). At the landscape level, the desert steppe vegetation conforms to the NEM: it does not respond to grazing but varied significantly from year to year, pointing at climatic variability as the primary driver of vegetation dynamics, as predicted by the NEM (WESCHE a. RETZER 2005; FERNANDEZ-GIMENEZ a. ALLEN-DIAZ 1999). The present study does not provide a time-series of vegetation development, but it can safely be assumed that climate-dependent interannual variations occur at the study sites (cf. ZEMMRICH et al. 2007). Through the detection of equilibrial properties WESCHE and RETZER (2005) and FERNANDEZ-GIMENEZ and ALLEN-DIAZ (1999) demonstrated that Mongolia's desert steppes are intermediate between equilibrium and nonequilibrium systems. This is confirmed for the community-level by the present study.

Our results show that non-equilibrial properties of Mongolia's desert steppes emerge most clearly at the landscape level, while at the community level they display an intermediate position between equilibrium and non-equilibrium ecosystems (cf. WIENS 1984; DEANGELIS a. WATERHOUSE 1987; BRISKE et al. 2003). At the population level, they conform to the equilibrium model. This divergence of response between scale levels is due to the fact that different ecological factors – like climate, competitive interactions, disturbance regimes, and soil properties – operate at different scales (WIENS 1989; O'NEILL 2001), thus confounding grazing impact across various spatio-temporal scales (FUHLENDORF a. SMEINS 1997). Furthermore, also vegetation properties function perceptibly at different scale levels and consequently will show different responses to grazing and climatic variability (BRISKE et al. 2003).

The present study shows that vegetation dynamics even in the extremely arid desert steppes of western Mongolia respond to grazing in both equilibrial and non-equilibrial ways, depending on the observational scale. These results corroborate the necessity of a multiple-scale approach for assessing vegetation dynamics and grazing impact in rangelands (FUHLENDORF a. SMEINS 1999; OBA et al. 2003). In a revised concept of rangeland ecosystems, which integrates the EM and NEM by applying them to different scales of observation, the crucial questions are: at which scale levels do specific system properties change from non-equilibrial to equilibrial? Are these scales levels and properties relevant to management strategies? The latter question, negated by SULLIVAN and ROHDE (2002), requires thorough research separately for each ecological zone. Applied to the present study, it leads to further questions: at which grazing intensity do Artemisia xerophytica populations become extinct? Which is the minimum population size A. xerophytica needs to reproduce sustainably under a variable rainfall regime? These questions could be answered by comparing arid landscapes that co-evolved with wild herbivores (e.g. Mongolia) with landscapes that evolved without (e.g. arid Australia; cf. HARRINGTON et al. 1984). The answer may help in understanding another crucial issue of rangeland ecology: to what extent is current vegetation secondary, a deviation from an original state? Did humans only replace wildlife with domestic animals, or was their ecological impact much greater?

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